The Beagle, Records of the Museums and Art Galleries of the Northern Territory, 2003 **19**: 137–142

Additional frogs from the mid-Miocene Camfield beds of Camfield Station, Northern Territory, Australia

MICHAEL J. TYLER [1], DIRK MEGIRIAN [2] AND LESTER RUSSELL [1]

[1] *Department of Environmental Biology*
University of Adelaide, SA 5005, AUSTRALIA
michael.tyler@adelaide.edu.au
[2] *Museum and Art Gallery of the Northern Territory*
GPO Box 4646, Darwin NT 0801, AUSTRALIA
dirk.megirian@nt.gov.au

ABSTRACT

Ilia determined to represent new species of the myobatrachid frog genera *Crinia* Tschudi and *Lechriodus* Boulenger have been located in the Camfield beds of the Northern Territory. *Crinia lacinia* sp. nov. and *Lechriodus bauzeorum* sp. nov. are described and additional representatives of the hylids *Litoria curvata* Tyler and *L. conicula* Tyler are reported. To date, all of the ilia in the Bullock Creek Local Fauna are from uniformly small individuals of estimated snout-vent lengths of around 30 mm. Data on the size distributions of extant species in the Northern Territory implies a reliable availability of moisture throughout the year at Camfield during Bullock Creek Local Fauna (mid-Miocene) times.

KEYWORDS: Myobatrachidae, Hylidae, *Crinia*, *Lechriodus*, ilia, fossil, new species, Miocene, Camfield beds, Northern Territory, palaeoenvironment.

INTRODUCTION

The original discovery of nine ilia resulted in the description of three new species of frogs from the mid-Miocene Camfield beds in the Northern Territory (Tyler 1994a). That publication constituted the first record of fossil frogs in the Northern Territory, and was also only the third recorded occurrence of fossil frogs in northern Australia. The Tertiary taxa previously described from the Camfield beds are all members of the family Hylidae, better known as tree frogs, although the family includes fossorial species. Two are members of the extant genus *Litoria* Tschudi and the third is a representative of the extinct genus *Australobatrachus* Tyler, 1976.

As a result of further collections by staff of the Museums and Art Galleries of the Northern Territory, 16 more ilia have been recovered from the Camfield beds. Described below are new species of the myobatrachid genera *Crinia* Tschudi and *Lechriodus* Boulenger, additional representatives of two of the hylid taxa described previously, plus an undetermined species of *Litoria* and one of *Crinia*. The frog fauna of the Camfield beds as it is now understood is summarised in Table 1.

The palaeoclimatic implications of the small body sizes of the Camfield beds frogs are explored by analogy with the distributional pattern of size classes in the modern Northern Territory fauna.

Table 1. Frogs of the Bullock Creek Local Fauna, Camfield beds of the Northern Territory.

Hylidae
Australobatrachus undulata Tyler, 1994a
Litoria conicula Tyler, 1994a
Litoria curvata Tyler, 1994a
Litoria sp. (this work)
Myobatrachidae
Crinia lacinia sp. nov. (this work)
Crinia sp. (this work)
Lechriodus bauzeorum sp. nov. (this work)

MATERIAL AND METHODS

The specimens reported here were extracted from fossiliferous Camfield beds limestone using dilute (~10%) acetic acid. Insoluble residues of acid digestion were passed through a set of screens (4.0, 2.0, 1.0 and 0.5 mm), which were then scanned under the microscope. Frog ilia were recovered only from the 2 mm screen. All specimens are deposited in the palaeontological collections of the Museum and Art Gallery of the Northern Territory (NTM).

Descriptive terminology of ilia follows the nomenclature adopted by Tyler (1976). Illustrations of these specimens were prepared on an Olympus SZH10 Research Stereomicroscope, fitted with an SC35 Type

Table 2. Yield of frog ilia relative to mass of fossiliferous limestone processed and mass of screenings surveyed. nd = no data.

Limestone batch	Quarry	Facies	Estimated mass of limestone processed (kg)	Mass of screenings (insoluble residues) >2mm, <4mm (g)	No. of frog ilia
P8697–	Dromornithid Mountain	conglomeratic limestone and calcimudstone	250	732	2
P87106–	Site Y	calcimudstone	nd	nd	1
P87113–	Site Y	calcimudstone	nd	nd	1
P87114–	Top Site	conglomeratic limestone and calcimudstone	100	219	1
P9215–	Top Site	calcimudstone	15	40	7
P9613–	Site X	calcimudstone	20	31	2
P9967–	Site X	calcimudstone	25	157	1
P9969–	Site X	calcimudstone	200	262	1
P9974–	Top Site	calcimudstone	40	215	2
P933–P938 inclusive	nd	nd	nd	nd	6
TOTAL ILIA					24

12 camera using a Sony UPC–2020 Black and White Printing Pack (Fig. 1A,B), and with a Ricoh Caplio RR30 digital camera (Fig. 1C,D).

The comparative osteological material of extant species used is housed in the Herpetological Laboratory of the Department of Environmental Biology at the University of Adelaide.

OCCURRENCE OF FROGS IN THE CAMFIELD BEDS

The Camfield beds, in the north central Northern Territory, consist of discontinuous outcrops of calcareous siltstone and sandstone, gypsiferous siltstone, limestone and cherty limestone (Randal and Brown 1967; Murray and Megirian 1992). The frog ilia described here, and those described previously by Tyler (1994a) were all collected from a *ca* 1 km^2 outcrop at about 17°7' S, 131°31' E. The outcrop and the various named fossil quarries which have produced frog ilia are depicted in Murray and Megirian (1992: fig. 3).

The Bullock Creek Local Fauna (LF) comes predominantly from conglomeratic limestone and calcimudstone facies of the formation, which Murray and Megirian (1992) interpreted as representing stream channel and lacustrine (oxbow) environments of a carbonate-depositing stream system. The Bullock Creek LF is considered to be mid-Miocene on the basis of marsupial stage-of-evolution biochronology (e.g. Woodburne *et al*. 1985; Rich 1991; Murray *et al*. 2000).

Frog ilia are infrequent in the Camfield beds, with only 24 specimens recovered so far. Approximately 650 kg of fossiliferous limestone yielded 16 of the specimens (Table 2). Of these, 13 were recovered from massive calcimudstone, and three from sites where conglomeratic limestone is associated with calcimudstone. (Two additional specimens (P87106–48, P87113–58) came from calcimudstone, but no data are available on the mass of limestone processed, and no sedimentological information or mass estimates are available for the quarried blocks that yielded specimens P933 to P938 inclusive – Table 2). The statement in Tyler (1994a) to the effect that the Top Site and Dromornithid Mountain quarries are in conglomeratic limestone requires clarification. Fossiliferous conglomeratic limestone is present at both these localities, but so too is fossiliferous calcimudstone, and both facies have been quarried. Bedding in the formation is poorly developed, and facies transitions are typically gradational. Consequently both facies may have been sampled in the same quarried block. Limestone batches P87114– (Top Site) and P8697– (Dromornithid Mountain) were at least in part conglomeratic, as indicated in Tyler (1994a). Batch P9974– (Top Site), however, was entirely calcimudstone (Table 2).

SYSTEMATICS

Order ANURA Rafinesque
Family Myobatrachidae Schlegel
***Lechriodus* Boulenger**
***Lechriodus bauzeorum* sp. nov.**
(Fig. 1A)

Material. HOLOTYPE – NTM P9215–2, proximal portion of a right ilium; Top Site, Bullock Creek Locality, Camfield Station, NT (17°00' S, 131°30' E); Bullock Creek Local Fauna, mid-Miocene.

Description of holotype. Only the proximal portion of the ilial shaft remains. The shaft is missing superiorly from a position approximately 0.5 mm

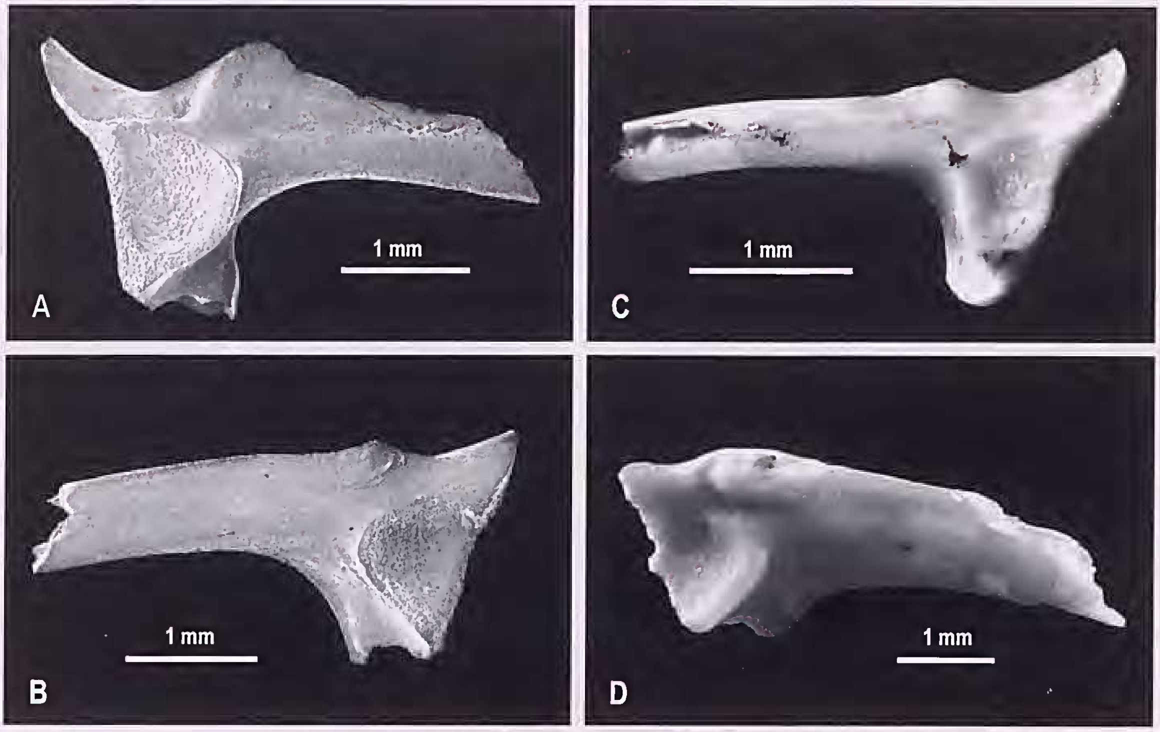

Fig. 1. **A**, Holotype of *Lechriodus bauzei* sp. nov. NTM P9215–2, right ilium in lateral view. **B**, Holotype of *Crinia lacinia* sp. nov. NTM P9215–14, left ilium in lateral view. **C**, *Crinia* sp. NTM P9215–17, left ilium in lateral view. **D**, *Litoria* sp. NTM P87113–58, right ilium in lateral view.

anterior to the acetabular fossa, and terminates inferiorly approximately 3.0 mm anterior to the fossa, nevertheless there is a sufficient amount of the shaft to exhibit the commencement of the broad, flaring dorsal crest so characteristic of the genus (Tyler 1976).

The acetabular fossa is large and well defined, with a narrow but prominent rim. The preacetabular zone is very narrow and the ventral acetabular expansion is incomplete but evidently well developed and slightly protrudes anteriorly, so creating a weakly sigmoid anterior profile.

The dorsal prominence and dorsal protuberance are not differentiated from the proximal portion of the ilial shaft. The dorsal acetabular expansion is complete, narrow and acutely pointed. It is separated from the shaft by a shallow depression.

Comparison with other species. Four extant and two extinct congeners are known. The extant species are *L. fletcheri* (Boulenger) of coastal south-east Australia and *L. melanopyga* (Doria), *L. aganoposis* Zweifel and *L. platyceps* Parker of New Guinea. Of these species, the Camfield specimen resembles the ilium of *L. aganoposis* most closely, differing principally in the dorsal crest arising at a point adjacent to the posterior margin of the acetabular fossa, whereas in *L. aganoposis* the dorsal crest arises adjacent to the posterior margin of the fossa (Tyler 1989: fig. 3D).

The two known extinct species are *L. intergerivus* Tyler, 1989 from the late Oligocene to mid-Miocene of the Carl Creek Limestone, Riversleigh Station, Queensland and *L. casca* Tyler and Godthelp, 1993 from the Early Eocene of Murgon, Queensland. Several hundred ilia of *L. intergerivus* have been recovered and it is evident from a comparison of the two taxa that the depth and extent of the flared ilial shaft of *L. bauzeorum* is proportionately more pronounced than in the former species. The preacetabular zone tends to be variable in shape but is more reduced in *L. bauzeorum* than in *L. intergerivus*.

In *L. casca* the flaring of the ilial shaft is greatly reduced (much less than in *L. bauzeorum*), but the lateral indentation of the shaft is more pronounced.

Comment. Although described from a single, incomplete bone, wider studies of extant and fossil species indicate clearly that ilial characters, and particularly the depth of the ilial shaft flange just anterior to the acetabular fossa, are reliably diagnostic (Tyler 1976, 1989; Tyler and Godthelp 1993).

Etymology. Named in honour of Robert and Elizabeth Bauze of Adelaide for the support that they have given to palaeontology.

Crinia **Tschudi**

Crinia lacinia **sp. nov.**

(Fig. 1B)

Material. HOLOTYPE – NTM P9215–14, proximal portion of left ilium. PARATYPES – P9215–3, left ilium; P9213–15, left ilium; P9215–16 right ilium. All from Top Site; other data as for *Lechriodus bauzeorum* (above).

Description of holotype. Ilial shaft slender and slightly curved (Fig. 1B). Lacks dorsal crest, but with shallow and poorly defined lateral indentation. Distal end of shaft incomplete, approximately one-half believed to be lacking, based upon comparing the distal portion with complete ilia of other species.

Acetabular fossa large and deep, and with prominent elevated rim. Dorsal margin of acetabular fossa entirely superior to inferior margin of ilial shaft. Preacetabular zone extremely prominent and expanding progressively inferiorly. Inferior margin of subacetabular expansion lacking. Dorsal acetabular expansion slightly raised. Dorsal prominence slightly raised and angular in profile. No evidence of dorsal protuberance. Length of specimen: 3.5 mm.

Description of paratypes. There are three paratypes – two left ilia, NTM P9215–3 and P9215–15, and a right, P9215–16. The shafts of P9215–3 and P9215–16 are broken at approximately the same position as the holotype, and their preserved lengths are 6.0 and 4.0 mm respectively. P9215–15 is more complete, but from a much smaller individual. Each is extremely similar to the features of the holotype, with a broad and evenly rounded preacetabular zone. The dorsal prominence is angular in profile in P9215–3 and rounded (possibly as a result of abrasion) in P9215–15 and P9215–16. The dorsal acetabular expansion is slightly raised in each of the paratypes.

Comparison with other species. With the exception of the extant species *Crinia remota* (Tyler and Parker), which has been found in a cave deposit of Holocene or late Pleistocene age, the only other fossil *Crinia* known is *C. presignifera* Tyler, 1991, from the late Oligocene or early Miocene of Riversleigh Station, Queensland. The nature of the preacetabular zone distinguishes the two species very clearly, for it is very poorly developed (scarcely extending beyond the anterior rim of the acetabular fossa) in *C. presignifera*, and very well developed in *C. lacinia*. Data on extant species are provided by Tyler (1976).

It is also likely that *C. lacinia* grew to a larger size than *C. presignifera*. An incomplete paratype of *C. lacinia* (P9215–3), measures 6.0 mm and the bone is estimated to have had a total length of around 11.0 mm or 12.0 mm. In contrast, the largest complete ilium of *C. presignifera* measures 7.1 mm (Tyler 1991).

Etymology. The Latin *lacinia* means a lappet or fringe, and here refers to the very broad preacetabular zone.

Crinia **sp.**

(Fig. 1C)

Material. NTM P9215–17, left ilium lacking approximately one-half of the shaft of the dorsal acetabular expansion and a significant portion of the preacetabular and subacetabular zones. Top Site; other data as for *Lechriodus bauzeorum* (above).

Comments. Identification is based upon the cylindrical form of the ilial shaft bearing a slight medial and longitudinal indentation, the ilial curvature, weak development of the dorsal prominence and posterior position of the acetabular fossa. Poor development of the preacetabular zone precludes the possibility of this species representing *C. lacinia*.

Family Hylidae Gray

Litoria **Tschudi**

Litoria curvata **Tyler, 1994**

Material. NTM P87106–48, left ilium; P9215–18, left ilium: all from Top Site. P9613–1, left ilium; 9613–2, right ilium; P9967–1, right ilium; P9969–1, left ilium: all from Site X. Other data as for *Lechriodus bauzeorum* (above).

Comments. All of the specimens have incomplete shafts. The least damaged is P9613–1 which has a length of 9.6 mm. All specimens exhibit the diagnostic features of the holotype, being an almost straight ilial shaft, a pronounced laterally projecting dorsal prominence, and a broad, flanged and evenly-curved preacetabular zone.

Litoria conicula **Tyler, 1994**

Additional material. NTM P9974–2, left ilium; Top Site, other data as for *Lechriodus bauzeorum* (above).

Comments. Previously known exclusively from the holotype taken at the Bullock Creek locality, this specimen resembles the holotype very closely and shares the distinctive dorsal prominence, which is triangular in profile.

Litoria **sp.**

(Fig. 1D)

Material. NTM P87113–58, right ilium; Site Y, other data as for *Lechriodus bauzeorum* (above).

Comments. This specimen differs from the two named fossil species of *Litoria* from the Camfield beds (and from other genera) in the very weak development of the dorsal acetabular expansion. The preacetabular zone is evenly rounded and the dorsal prominence is not pronounced, but is abraded laterally and its actual shape is uncertain. Comparison has been made with a large collection of extant species without finding any evidence of affinity to any of the species groups recognised by Tyler and Davies (1978).

DISCUSSION

One of the more significant questions that can be posed about the Camfield beds is the nature of the mid-Miocene landforms, and the climate at the time that the fossil material was deposited. Because frogs lose water rapidly through their skin they have to either remain in contact with moisture, or avoid exposure to aridity. It follows that an understanding of the likely ecological requirements of the various frog taxa recovered will contribute to the interpretation of the nature of the mid-Miocene environment at Bullock Creek.

Following Bureau of Meteorology (1989), the present climate of the Northern Territory can be described in general terms as follows. The northern half (i.e. north of *ca* 20° S) lies in the 'summer rainfall – tropical' climatic zone. Summers are characterised by heavy periodic rains (heavier in coastal and elevated areas), with generally hot and humid conditions. Winters are generally rainless, mild to warm, and dry. The southern half of the Northern Territory lies in the 'arid' (mainly summer rain) – 'subtropical' climatic zone. Summers are characterised by variable rain, hot to extremely hot and very dry conditions, while winters are characterised by irregular light rain, mild to warm and dry conditions.

The transition from the one climatic zone to the other is not abrupt, but bisects a fairly even, more or less latitudinal climatic gradient, consistent with the lack of major influential physiographic features (e.g. high mountain ranges, rift valleys, inland seas, etc.). Median annual rainfall grades from about 1600 mm on the north coast to less than 200 mm at the Northern Territory / South Australia border, with average annual temperatures grading from about 27°C in the north to 21°C in the south. An additional significant gradient in relation to the present discussion is the annual rainfall variability, which is low to moderate in the Top End, and extreme in the south. Thus, the north experiences marked seasonal (winter) aridity with reliable summer rain, whereas the south is subject to low, highly irregular rainfall and extended periods of drought.

Tyler (1994b) found that in the Northern Territory, frog species diversity correlates strongly with median annual precipitation, which is consistent with the findings of Pianka and Schall (1981) for the whole continent. Pianka and Schall (1981) examined vertebrate species diversity in relation to five climatic variables, and found that for frogs, species diversity correlated only (though strongly) with median annual rainfall. The 24 known frog ilia from Bullock Creek represent seven species (five determined and two undetermined at species level). Unfortunately, the available sample size is too small to reach any conclusion about what the total frog diversity at Bullock Creek might have been during Bullock Creek LF time (mid-Miocene), and thereby permit an estimation of the possible median annual precipitation.

Tyler (1994b) also found that the size of frogs in the Northern Territory was inversely correlated to median annual precipitation. The relationship of frog size to average annual temperature was not examined, but given that both median annual precipitation and average temperature decrease toward the south through the Northern Territory, as outlined above, it could be expected that a similarly strong inverse correlation exists between frog size and average annual temperature. In terms of physiological capacity to handle water stress, a preponderance of smaller frogs at northern Northern Territory latitudes is perhaps more significantly correlated to the presence of reliable moisture in the environment throughout the year. In the Northern Territory analogy, places with reliable surface moisture are not sustained by direct precipitation throughout the year, rather they are sustained by regional groundwater discharge and soil moisture during the dry season. Elsewhere in Australia, small frogs are also found in uniform rainfall zones. While small frogs may be indicative of the presence of reliable moisture in the environment, they are uninformative about rainfall distribution over the seasonal cycle.

The uniformly small size of the Camfield beds frogs is therefore an indication of the presence of permanent moisture in the depositional environment, which is consistent with the presence of a diverse aquatic element (crocodilians, chelid turtles, teleost fish, lungfish, aquatic molluscs, ostracods, charophyta, cyanobacterial stromatolites) in the Bullock Creek Local Fauna (Murray and Megirian 1992). The fossil frogs, with estimated *ca* 30 mm snout-vent lengths, were smaller on average than those present today in the north of the Northern Territory (=38 mm, Tyler 1994b), suggesting that the Bullock Creek palaeoclimate was physiologically less stressful on frogs than the present most optimal environments of, for example, Kakadu in the northern Northern Territory. This inference is consistent with some other palaeoclimatic data. For example, during the mid-Miocene, Bullock Creek was at about latitude 30° S (i.e. about 13° further south than today), and sea-surface temperatures around the continent were about 18°C (e.g. Savin *et al.* 1985). This indicates that latitudinal temperature gradients across the continent were probably considerably lower than today, with mild to warm conditions throughout, rather than cool to mild in southern parts and warm to hot in northern parts as it is today.

Tyler (1994a) hypothesised that seasonal aridity was probably not a feature of Bullock Creek palaeoclimate, citing the small size of frogs and absence of fossorial species as evidence. On the other hand, Murray and Megirian (1992) attributed the uniformly small size of teleost fishes in the Camfield beds to seasonal aridity. In the light of the preceding discussion, the presence of small frogs does not exclude the possibility of seasonal aridity.

The presence of only one specimen of *Lechriodus* in the fauna merits comment because there is a progressive reduction in the incidence of this genus from the Oligocene in the Carl Creek Limestone at Riversleigh, north-western Queensland (Tyler *et al.* 1990), and this reduction has been interpreted to be a consequence of environmental change. Riversleigh at 19° S is at similar latitude to Bullock Creek (17° S), and their positions relative to each other were constant throughout the Tertiary. In the earliest of the Riversleigh sites where there are adequate sample sizes, the incidence of *Lechriodus* in the frog fauna is as high as 80.8%. At the youngest site the incidence is only 35.5%. Sample sizes at the various sites ranged from 17 to 110. The one specimen in the Bullock Creek Local Fauna equates to 4% of the total individuals recovered. It is tempting to suggest that the proposed demise of the Riversleigh frogs (attributed to a reduction in forest habitat in response to increasing aridity) applied equally to Bullock Creek at a similar time.

ACKNOWLEDGMENTS

We express our appreciation to the many people who have contributed over the years to our investigations of the Camfield beds, and to the referees, Drs Michael Mahoney and Margaret Davies.

REFERENCES

Bureau of Meteorology, 1989. *Climate of Australia*. Bureau of Meteorology, Department of Administrative Services: Canberra.

Murray, P. and Megirian, D. 1992. Continuity and contrast in middle to late Miocene vertebrate communities in the Northern Territory. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* **9**(1): 195–218.

Murray, P., Megirian, D., Rich, T., Plane, M., Black, K., Archer, M., Hand, S. and Vickers-Rich, P. 2000. Morphology, systematics, and evolution of the marsupial genus *Neohelos* Stirton (Diprotodontidae, Zygomaturinae). *Museums and Art Galleries of the Northern Territory Research Report 6*.

Pianka, E.E. and Schall, J.J. 1981. Species densities of Australian vetebrates. In: Keast, A. (ed.) *Ecological biogeography of Australia*. Pp 1676–1694. Dr W. Junk Publishers: The Hague.

Randal, M.A. and Brown, M.C. 1967. The geology of the northern part of the Wiso Basin, Northern Territory. *Bureau of Mineral Resources, Geology and Geophysics, Australia, Record* 1967/110.

Rich, T.H. 1991. Monotremes, placentals, and marsupials: their record in Australia and its biases. In: Vickers-Rich, P., Monaghan, J.M., Baird, R.F. and Rich, T.H. (eds) *Vetebrate palaeontology of Australasia*. Pp 893–1070. Pioneer Design Studio and Monash University Publications Committee: Melbourne, Australia.

Savin, S.M., Abel, L., Barrera, E., Hodell, D., Keller, G., Kennett, J.P., Killingley, J., Murphy, M., and Vincent, E. 1985. The evolution of Miocene surface and near-surface marine temperatures: Oxygen isotope evidence. In: Kennett, J.P. (ed.) *The Miocene ocean: paleoceanography and biogeography*. Pp 49–82. Memoir **163**: Geological Society of America: Colorado.

Tyler, M.J. 1976. Comparative osteology of the pelvic girdle of Australian frogs and description of a new fossil genus. *Transactions of the Royal Society of South Australia* **100**: 3–14.

Tyler, M.J. 1989. A new species of *Lechriodus* (Anura: Leptodactylidae) from the Tertiary of Queensland, with a redefinition of the ilial characteristics of the genus. *Transactions of the Royal Society of South Australia* **113**: 15–21.

Tyler, M.J. 1991. *Crinia* Tschudi (Anura: Leptodactylidae) from the Cainozoic of Queensland, with the description of a new species. *Transactions of the Royal Society of South Australia* **115**: 99–101.

Tyler, M.J. 1994a. Hylid frogs from the mid Miocene Camfield Beds of northern Australia. *The Beagle. Records of the Northern Territory Museum of Arts and Sciences* **11**: 141–144.

Tyler, M.J. 1994b. Climatic change and its implications for the amphibian fauna. *Transactions of the Royal Society of South Australia* **118**: 53–57.

Tyler, M.J. 1976. Comparative osteology of the pelvic girdle of Australian frogs and description of a new fossil genus. *Transactions of the Royal Society of South Australia* **100**: 3–14.

Tyler, M.J. 1989. A new species of *Lechriodus* (Anura: Leptodactylidae) from the Tertiary of Queensland, with redefinition of the ilial characters of the genus. *Transactions of the Royal Society of South Australia* **113**: 15–21.

Tyler, M.J. and Davies, M. 1978. Species groups within the Australopapuan hylid frog genus *Litoria* Tschudi. *Australian Journal of Zoology* Supplementary Series **63**: 1–47.

Tyler, M.J. and Godthelp, H. 1993. A new species of *Lechriodus* Boulenger (Anura: Leptodactylidae) from the early Eocene of Queensland. *Transactions of the Royal Society of South Australia* **117**: 187–189.

Tyler, M.J., Hand, S.J. and Ward, V.J. 1990. Analysis of the frequency of *Lechriodus intergerivus* Tyler (Anura: Leptodactylidae) in Oligo-Miocene local faunas of Riversleigh Station, Queensland. *Proceedings of the Linnean Society of New South Wales* **112**: 105–109.

Woodburne, M.O., Tedford, R.H., Archer, M., Turnbull, W.D., Plane, M.D. and Lundelius, E.L. 1985. Biochronology of the continent mammal record of Australia and New Guinea. *Special Publication of the South Australian Department of Mines and Energy* **5**: 347–363.

Accepted 16 October 2003